SOME ADDITIONS TO OUR KNOWLEDGE OF ANTIARCHS

by D. M. S. WATSON

ABSTRACT. The author has in his collection some uncrushed antiarch material which is very beautifully preserved. This has enabled him to determine the shape of *Bothriolepis* with real certainty, and to describe the muscle insertions on the helmet process, and thus interpret their function. The material also shows the opercular plate, and its relation to the branchial cavity, thus suggesting the probable nature of the gill arches, and enabling them to be compared with those of other groups.

THE remarkable group of Old Red Sandstone 'fish', the Antiarchi, of which the oldest known member is *Pterichthyodes*, has now been very completely described and analysed by a succession of authors, from Agassiz who named *Pterichthyodes* [*Pterichthys*], and Eichwald who named *Asterolepis* and *Bothriolepis*, to Stensiö. Traquair (1894) made out the external structure of the limb in many forms; Gross (1931) gave an admirable account of the structure and mechanics of the limb in *Asterolepis*; Stensiö (1948, 1959) has given a full and detailed account of the Canadian *Bothriolepis canadensis*; but some material in my own collection, from Russia and Scotland, seems to add a little to our knowledge, especially of the musculature of the limb, and the shape of the body.

SHAPE OF BODY

Bothriolepis panderi Lahus (P. 533) from the D_3^1 Shelon Beds, Syas River, Stolbovo, U.S.S.R., given me by Professor Obruchev, is remarkable because it is very little crushed or distorted (text-fig. 1). Although its right side has suffered a little depression it still, taken as a whole, shows the real shape of the head and anterior part of the body more clearly than any other individual known to me. Furthermore, it is a very small (i.e. young?) individual, the total width across the head shield being of the order of 4 cm., in contrast to some 6·5 cm. in a rather small *B. canadensis*. It is of markedly pentagonal section across the body; the ventral surface, which rounds into the lateral surfaces, is essentially flat, the side walls pass upwards and outwards, and there is a distinct median ridge along the anterior median dorsal plate, continued eventually on the incomplete posterior median plate. Gross's reconstruction of *Asterolepis* (1931) is an admirable illustration of the shape of this form, which is somewhat deeper, and is confirmed by the evidence of a small specimen from Nairn of *A. maxima* (P. 67) also complete and undistorted.

PECTORAL FIN

Specimen P. 533 has the beautifully preserved proximal part of each arm in articulation with its helmet process (Stensiö's *processus brachialis*). The arms lie closely along the sides of the body in an extreme backward position, and slope down towards the bottom. The denticulated hinder border of the arm plate for most of its length is separated from the ventrolateral plate by a small space of the order of a millimetre, the arm becoming progressively flattened as it approaches the elbow. The helmet process of the

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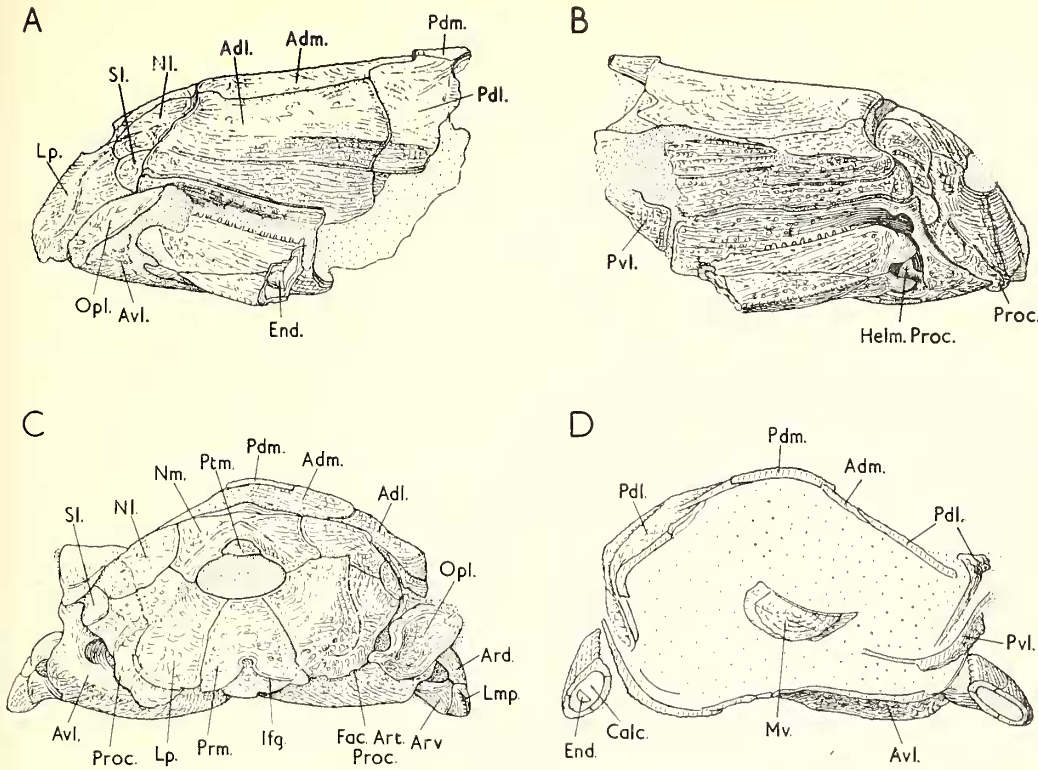
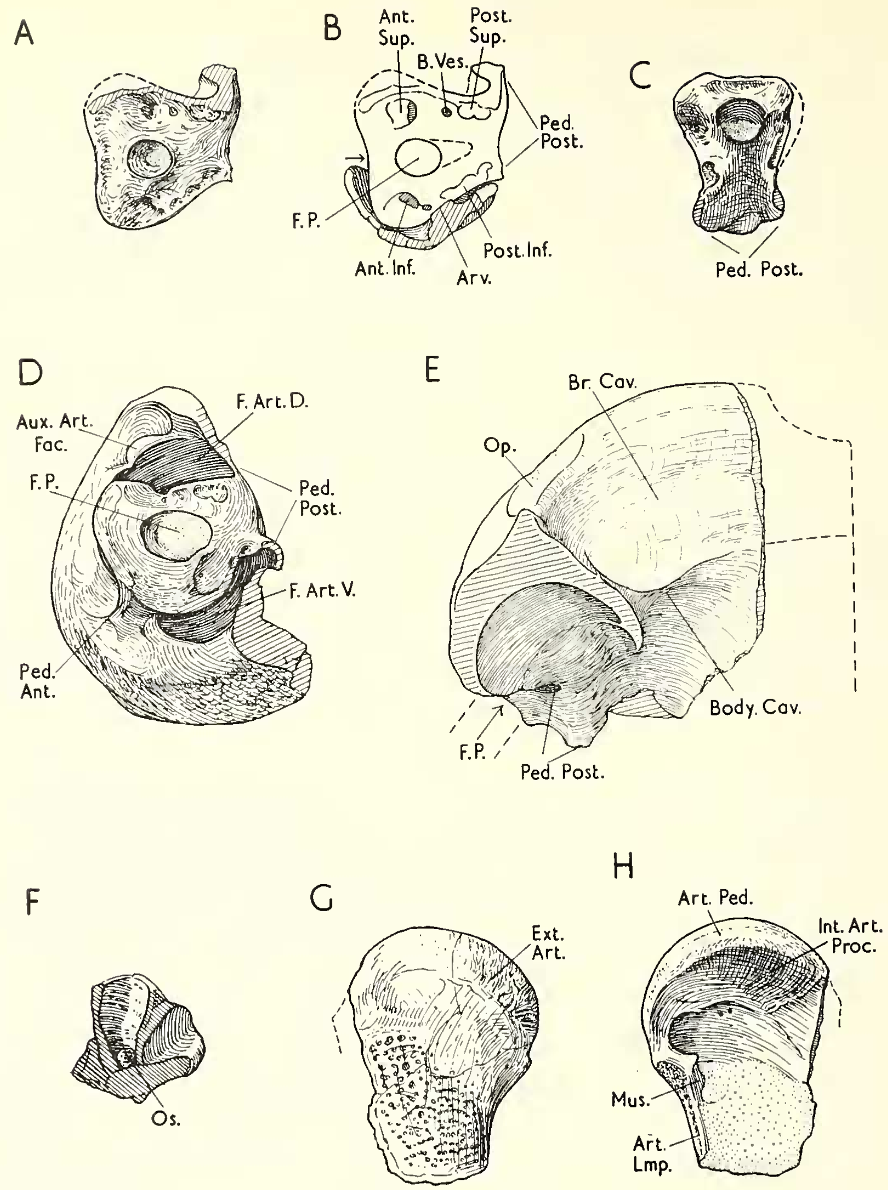


TEXT-FIG. 1. *Bothriolepis panderi* Lahus, P. 533, Upper Devonian, D_3^1 Shelon Beds, right bank of Syas River, Stolbovo, U.S.S.R., collected by Professor D. Obruchev; natural size.

The anterior end of a small individual, essentially uncrushed, which shows the shape of the animal better than any other I have seen; *A*, left lateral, *B*, right lateral, *C*, anterior, *D*, posterior aspects.

The gill chamber is here uniquely preserved; the left operculum is present, a little misplaced dorsally and posteriorly, the right is absent, exposing the posterior wall of the gill chamber which is carried on the anterior ventro-lateral. The rounded process of the lateral plate which fits into the opercular notch is well shown on the right side; it is partly hidden on the left by the inturned anterior projection of the opercular. Both pectoral appendages are in natural articulation, brought as close to the body as possible. The left shows the presence in section of a hollow structure (*End.*), which is D-shaped, and appears to represent a cartilaginous axis with a superficial investment by bone. Between this axis and the superficial bone the upper half of the cavity is completely filled with a white calcareous mass, obviously deposited from solution in an empty space. The lower part of the cavity, including that within the axis, is filled by red mud. The right arm is cut across farther along its length, but contains two quadrangular pieces of the white calcareous infilling described above, embedded in a normal red mud infilling. The helmet process, obscured by matrix on the left side, is well seen on the right, where the wide space between the articular parts of the two proximal arm plates shows how considerable was the freedom of motion up and down, and presumably rotationally, of the arm. *Adl.*, anterior dorso-lateral; *Adm.*, anterior median dorsal; *Ard.*, dorsal articular; *Arv.*, ventral articular; *Avl.*, anterior ventro-lateral; *Calc.*, calcite infilling in arm; *End.*, axial skeleton of arm; *Fac. Art. Proc.*, seating for the articular process of the opercular; *Helm. Proc.*, helmet process; *Ifg.*, infraorbital sensory canal groove; *Lmp.*, lateral marginal; *Lp.*, lateral; *Mv.*, median ventral; *Nl.*, lateral nuchal; *Nm.*, median nuchal; *Opl.*, opercular; *Pdl.*, posterior dorso-lateral; *Pdm.*, posterior median dorsal; *Prm.*, premedian; *Proc.*, the rounded process of the lateral plate which fits into the notch of the opercular; *Ptm.*, post median; *Pvl.*, posterior ventro-lateral; *Sl.*, sufflaminal.



TEXT-FIG. 2. Five fragments of *Bothriolepis*, Upper Old Red Sandstone, Moray, Scotland, natural size.

A, *Bothriolepis sp.*, P. 777*a*, ? Scaat Craig, left helmet process seen from the side. *B*, outline of the same, with the muscle insertions shown in plan, and the proximal end of the ventral arm plate belonging to it (P. 777b) in place, broken through an internal muscle insertion; the extent of the funnel pit is shown by a dotted line; an arrow shows the position of the thin anterior end of the pedicel (Stensiö's *pars pedalis*) and the triangular muscle insertion distal to it. *C*, *Bothriolepis sp.*, P. 779, ? Scaat Craig, right helmet process (orientated to show up surface modelling and the muscle insertions). *D* and *E*, *Bothriolepis major*, P. 625, Scaat Craig, exceptionally large left anterior ventro-lateral plate showing right arm is widely exposed through the large notch between the dorsal and ventral proximal arm plates, which are rigidly attached to one another. The ventral arm plate is in contact with the thin anterior end of the pedicel (Stensiö's *pars pedalis*) of the helmet process, and in this position the outer border of the arm is so far downturned that it alone—if resting on a hard surface—can touch the lake bottom. But, as I shall shortly show, the dorsal arm plate could equally well be in similar contact with the pedicel, thus indicating that the arms were capable of twisting round on their own axes on the helmet process through an angle which may be some 30 degrees; in which case the broad plane of the arm may have stood almost vertically, nearly parallel to the principal plane of the body. In this position the swimming stroke would be effective, whilst in the other extreme position the limb could be brought forward with the least possible resistance from the water.

Articulation. The general position of the helmet process in relation to the animal as a whole, which has long been known, and its implications in the determination of the plane of movement of the limb understood, is exceedingly well shown by Stensiö (1931, figs. 40–42), and it is evident that there is an extraordinarily accurate fit of the proximal arm plates on the helmet process. Furthermore, Gross (1931) has determined the possible movements of the pectoral fin on the helmet process. I have, however, a beautifully preserved specimen of *Bothriolepis* (P. 777*a* and *b*), from ? Scaat Craig, the famous Upper Old Red Sandstone locality in Moray, Scotland, which shows the fit of the arm plates on the helmet process unusually well. It consists of a helmet process broken off from its pedicel, and one of the arm plates which clasped it, separated and entirely free from matrix, and in consequence shows by trial the extremely accurate way in which the arm plate slides round the process, maintaining contact despite the lack of soft parts (text-fig. 2, *A* and *B*). Its range of sliding movement is through about 90 degrees, agreeing with that assumed from the evidence of complete specimens with arms in articulation.

At the same time it shows that there is some possibility of rotational movement, for the pedicel is narrow anteriorly, and broadens towards the inturned posterior surface, so that it is wedge-shaped in section. This is particularly well shown in P. 625, a magni-

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the helmet process somewhat damaged, collected by Professor S. P. Welles; *D*, from behind and slightly below, showing the unusual auxiliary articular facet; *E*, from above, showing the floor of the branchial chamber, and the anterior wall of the body cavity. *F*, *Bothriolepis sp.*, P. 778, ? Scaat Craig, helmet process split through the length of the funnel pit, which received the skeletal axis of the pectoral fin, showing the ossified base (*Os.*).*G*, and *H*, *Bothriolepis sp.*, P. 783, ? Scaat Craig, proximal end of right ventral arm plate *G*, outer, *H*, inner face showing the surface for articulation with the helmet process. *Ant.Inf.*, antero-inferior muscle insertion; *Ant.Sup.*, antero-superior muscle insertion; *Art. Lmp.*, articular surface for lateral median plate; *Art. Ped.*, articular surface on pedicel; *Arv.*, ventral articular plate of arm (reference line ending in a thickening which is a muscle insertion); *Aux. Art. Fac.*, auxiliary articular facet; *B. Ves.*, blood-vessel; *Body Cav.*, base of partition separating the gill chamber from the body cavity; *Br. Cav.*, branchial cavity; *Ext. Art.*, articular surface of proximal arm plate for the outer side of the groove around helmet process; *F. Art. D.*, upper sliding surface for articulation of fin; *F. Art. V.*, lower sliding surface for articulation of fin; *F. P.*, funnel pit; *Int. Art. Proc.*, internal articulation on sliding surface of helmet process; *Op.*, facet for free margin of operculum; *Os.*, ossification at base of funnel pit; *Ped. Ant.*, anterior and outer (thin) end of pedicel; *Ped. Post.*, posterior and inner (thick) end of pedicel; *Post. Inf.*, postero-inferior muscle insertion; *Post. Sup.*, postero-superior muscle insertion.

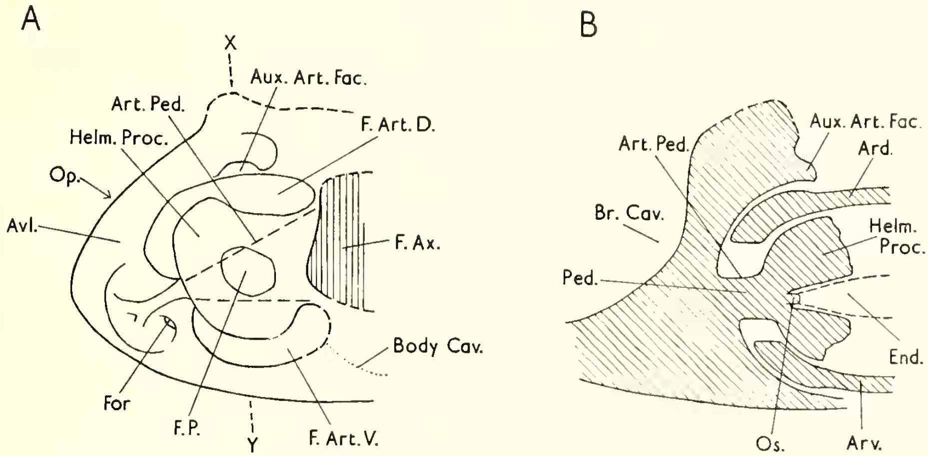
ficent helmet process still attached to part of the anterior ventro-lateral plate, completely free from matrix, which Professor S. P. Welles found during the vertebrate palaeontology excursion associated with the International Geological Congress of 1948, and very generously gave to me (text-fig. 2, *D* and *E*). In this specimen the pedicel widens from 3·3 mm. at its anterior and outer end to 12·0 mm. posteriorly, 20 mm. separating these points. The bearing surfaces on the pedicel for the arm plates (text-fig. 3, *Art. Ped.*) form segments of circles, and are quite flat, the helmet process swelling out distal to them, so that the arm was held in place by the contact between the opposed spheroidal surfaces of the helmet process and the inner sides of the two arm plates. These spheroidal surfaces are unequal in size, the upper being noticeably wider and longer than the lower, as shown in all available specimens. The 'slot' between the arm plates for the helmet process is not parallel sided, nor tight fitting, a condition shown by Traquair (1904, figs. 60–61), and confirmed by Gross (1931, pl. 6, figs. 1–2).

Thus it is evident that the arm plates embrace the helmet process by concave surfaces allowing sliding movement in one plane of up to 90 degrees, and also rotational movement in directions limited by the wedge-shaped pedicel, which, even at its widest, is less than the widest part of the 'slot'. In the fully advanced position of the arm, when it stands out at right angles to the body, the 'slot' would be held on the thick end of the pedicel, and the arm would be incapable of rotation (and probably of up and down movement). But when it was drawn back nearly parallel to the body, its 'slot' would surround the thin end of the pedicel, which would provide the conditions necessary for the small rotation of the arm on its axis, perhaps altering the direction of the fin through a small arc. This movement, of course, would have the effect of elevating or depressing the anterior border of the fin, enabling the animal to rise or fall in the water. The tail was obviously capable of enabling the animal to travel forward without the assistance of its pectoral fins, and such was presumably its normal method of progress from place to place.

The small size of the mouth parts, described by Stensiö (1931, fig. 74) in *B. canadensis*, implies that it ate food particles, and the essentially uncrushed P. 533 makes it clear that the mouth must lie immediately behind the anterior border of the head shield and face directly downward, so that the animal was a bottom feeder, browsing, as it were, on the floor of the lake or river in which it was living.

Auxiliary articular surface. One very curious feature of P. 625, less well shown in P. 780 (a fragment), is the presence on the anterior ventro-lateral, immediately above the highest point of the bearing surface for the upper arm plate, of a smooth apparently articular surface, agreeing exactly in character with that of the helmet process, called by Gross (1931, p. 16) 'siebknocken', and described by him as characteristic of movable joints. This area (text-fig. 2, *D*) lies as a low boss projecting from the floor of a semicircular depression, which dorsally passes abruptly to the outer surface of the bone, whilst anteriorly it grades into it over a rounded surface. The implication is that, when raised to its highest position, the outer surface of the upper arm plate actually came to bear upon it, though it is difficult from articulated specimens (e.g. P. 533) to understand how this could have come about.

Musculature. The general nature of the anterior ventro-lateral plate is well known and may be understood from Stensiö's account (1931). It should be noted that the large opening (*F.Ax.*) behind the helmet process, shown by Stensiö (1931, fig. 40), is peculiar to *Bothriolepis*, and is represented as a very much smaller opening in *Pterichthyodes* where, in an individual whose body carapace is 80 mm. long (C. 44, U.C.L. Coll.) it measures 3·2 mm. by a maximum of 2·5 mm.; in another specimen (C. 88), in which the carapace is 91 mm. long, the opening is 5·5 mm. by 2·1 mm. Such foramina are appropriate to house the artery and vein passing out into the limb, but are quite unsuitable in both size



TEXT-FIG. 3. *Bothriolepis major*, P. 625, Scaat Craig. Diagrammatic drawings of a left anterior ventro-lateral plate to illustrate the articulation of the arm with the helmet process, natural size.

A, seen postero-laterally, the position of the articular surfaces of the pedicel is shown by broken lines; *B*, section approximately through X–Y, the ossification in the funnel pit restored from P. 778, the proximal arm plates restored from other specimens; the arm is in its most forward position.

Ard., dorsal articular plate of arm; *Art. Ped.*, articular surface on the pedicel; *Arv.*, ventral articular plate of arm; *Aux. Art. Fac.*, auxiliary articular facet; *Avl.*, anterior ventro-lateral plate; *Body Cav.*, a line of dots showing the thickness of the bone, and the extent of the body cavity; *Br. Cav.*, branchial cavity; *End.*, axial skeleton of arm; *F. Art. D.*, upper sliding surface for articulation of fin; *F. Art. V.*, lower sliding surface for articulation of fin; *F.Ax.*, foramen axilare; *F.P.*, funnel pit; *For.*, foramen; *Helm. Proc.*, helmet process; *Op.*, facet for free margin of operculum; *Os.*, ossification at base of funnel pit; *Ped.*, pedicel.

and character to permit of the passage of a muscle as well. It seems, therefore, that the whole musculature of the pectoral fin must be internal, lying within the cavity of the fin and in general distal to the helmet process.

Of the six helmet processes of *Bothriolepis* in my collection, one was collected at Scaat Craig, and the others in all probability came from that locality; they represent, in fact, individuals which lived effectively together. The only other helmet process I possess is one of *Asterolepis* (P. 177) from Livonia, which affords a little confirmatory evidence. The detailed shape of the helmet process may be seen in text-fig. 2, *A–D*, which supplement various published figures, of which perhaps the best are those by Stensiö (1931) and Gross (1931, pl. 7), and show the nature of most of the muscle attachments. The surface facing into the cavity of the arm is finished with a thin layer of hard, smooth bone on which muscle insertions take the form of deep, sharply defined pits with a striated or otherwise roughened attachment surface, presumably for ligaments. It is cut off by the spheroidal sliding surfaces (*F. Art. D.* and *F. Art. V.*) for the proximal arm plates, which bear a characteristic ornament of very delicate, abruptly truncated grooves ('siebknocken') identical with the surfaces of the arm plates which slide on them. I do not know anything in modern vertebrates exactly comparable with these articular surfaces, and it is not at all easy to suggest how they arose.

The central funnel pit in my specimens is rather more than 6 mm. in diameter, and not always accurately circular; but its irregularities are not consistent, sometimes the hole is asymmetrical in shape, as in the original of text-fig. 2, *D*, sometimes effectively circular, as in text-fig. 2, *A* and *C*. The pit passes down between the sliding surfaces, is conical in section, and in the one case in which its proximal end is well shown (P. 778, text-fig. 2, *F*) bears a small, firmly attached, upstanding cylinder of bone, rising free for about a millimetre and separated from the walls of the pit by an annular space less than half a millimetre in width. The implication is that this pit housed a cartilaginous axial rod continuing into the arm, as we know from the occasional occurrence of a bony skin coating it, shown in text-fig. 1, *D*, and by Stensiö (1931, fig. 55), and confirmed by the presence in P. 176 of a very thin-walled cylinder of bone, which at its maximum is a little under 3 mm. high, in an arm of about 28 mm. across. How far it extended, and how far it served muscle attachments is unknown.

There are five muscle insertions on the helmet process, four of which, on its distal surface, are shown in text-fig. 2, *A–D*. The fifth is on its anterior face immediately distal to the anterior part of the pedicel, and lies just within the cavity included by the arm plates.

Of the insertions on the distal surface the most pronounced are the antero-superior and antero-inferior, which lie respectively above and below the funnel pit, near the front end where the distal surface is widest. These, which are seen on all the available material of *Bothriolepis*, are each divided into two parts, having a deep insertion, from which a slope passes forward reaching the surface of the helmet process abruptly. The postero-superior muscle insertion is well marked in all the individuals of my series. It is a single attachment, often deeply incised, and lying well back towards the opening of the foramen axillare. The postero-inferior insertion varies somewhat in appearance; in all cases it extends over a considerable distance, and is often divided into three parts. A foramen, or a small group of foramina, evidently for blood-vessels, lies between the insertion of the antero- and postero-superior muscle insertions.

The muscle attachment on the anterior face of the helmet process, well shown in *Asterolepis* by Pander (1857, pl. 6, fig. 2; pl. B, figs. 8*a* and *b*), occupies part of an equilateral triangle, lying between the sliding surfaces of the proximal arm plates, the anterior edge of the pedicel which separates them, and the thin, effectively straight, anterior edge of the distal surface of the helmet process. About half-way, or rather more, down the triangular area is a depressed region which is evidently the base of the muscle attachment; its surface is not very different in character, but the foramina which open into it seem to be a little larger than elsewhere, suggesting an increased provision of blood. This area is visible in all the helmet processes available, though it varies slightly, and is best shown in P. 777*a* and P. 779. Its relation to the arm as a whole is well shown on the right side of P. 533, though it is partly obscured by the lower proximal arm plate.

My three proximal arm plates of *Bothriolepis* from ? Scaat Craig show something of the inner surface and muscle attachments. One, P. 777*b*, a left, was found in position on its helmet process, is thus known to be a ventral plate, and agrees well with Gross's figure of *Asterolepis*. Towards the posterior edge it shows a muscle insertion in the form of a flat-topped, sand-eroded thickening, arising rather abruptly from the inner surface just distal to the articular part of the bone lying, in fact, within about 3 mm. of the outer surface of the helmet process (text-fig. 2, *B*). A deep groove proximal to the muscle insertion, and distal to the articulation with the helmet process, has the appearance of housing a blood-vessel. P. 783, a right arm plate (text-fig. 2, *G* and *H*), is shown by comparison with Stensiö's photograph of *Asterolepis* (1931, fig. 60, *B*) also to be a ventral plate, and agrees with P. 777*b* in the general character of its articular surface. But the comparable muscle insertion is not eroded and faces inwards and distally, and it may be noted that the groove just above the reference line *Mus.* is much deeper than in P. 777. P. 799 is a fragment of a proximal arm plate broken along its length, is probably a ventral, and if so is of the left side. It shows, just distal to the articular surface for the helmet process, a very definite, well preserved muscle insertion forming an irregular bony projection rising abruptly from the inner surface of the plate and facing mesially and distally, thus confirming the condition in P. 783. Stensiö's figures of the dorsal articular plates of *Asterolepis* (1931) show a possible muscle insertion lying on the inner surface just below the articular extremity on the admesian side; nothing similar is shown in his figure of ventral plates. Gross (1931, pl. 6, fig. 12) shows a muscle insertion labelled '*a*', which lies on the inner side of the dorsal plate just distal to its articulation with the helmet process.

It seems quite certain that the antero-superior and antero-inferior muscle insertions on the helmet process imply the presence of a dorsal muscle and a ventral one, which must be attached to the inner surface of the arm. The character of these insertions, with their deep basal part and sloping anterior surface, implies that the muscles were directed somewhat laterally, and would thus be attached to dorsal and ventral proximal arm plates respectively, not far from the sliding surfaces. Their joint shortening must pull the arm as a whole forwards, sliding the proximal part of the arm plate backwards round the helmet process, and the action of one alone could rotate the arm slightly on its own axis, a function obviously necessary if the arm is to be used as an oar. The corresponding posterior pair of insertions gives no similar indication of the direction in which the muscles attached to them came out, but the muscles must have passed into the cavity of the arm, and on contraction have had the effect of sliding the arm plate round so that the arm was pulled backward to lie alongside the body.

It will be seen from text-fig. 2, *B* that the muscle insertions on the distal surface of the helmet process only form part of a circle round the funnel pit, and lie in the main behind its centre. It is evident on mechanical grounds that some musculature must be provided to occupy the other half of the circle, and this, presumably, is the function of the muscle which arises from the triangular depression on the front face of the helmet process, immediately lateral to the thin end of its pedicel. The presence of the abrupt edge of the depressed area, and the pitch of the definite roughenings within it, show that a muscle arising from it must have passed outwards over the anterior border of the distal face of the helmet process to be attached to the inner surface of the proximal plates of the arm, and it must be the contraction of this muscle which draws the whole arm forwards without tending to twist it round on its axis.

When the lower proximal arm plate P. 777*b* is rearticulated with its helmet process, it is clear that the muscle suggested by the insertion on it cannot have arisen from the helmet process. As the attachment area is large, it is natural to assume that the muscle also was important, and it may possibly have accommodated some of the muscles which moved the distal part of the limb; but only examination of a series of well-preserved arm plates can make clear the nature of this musculature.

The right appendage of P. 533 shows beautifully that at its articulation the whole structure is very nearly circular; by the end of the anterior ventro-lateral plate it is 11·0 mm. wide but has already decreased to a depth of 4·6 mm., whilst the arm of the other side, 14·0 mm. from its articulation, is 11·0 mm. wide and 6·0 mm. in depth, thus showing the rapid flattening.

The most striking fact which arises from the whole discussion is the conclusion that the resemblance of the *Bothriolepis* arm to an arthropod limb really implies a similar musculature, of a kind not found in any other group of vertebrates; this is interesting as emphasizing the extreme versatility of chordate anatomy.

OPERCULAR

Bothriolepis panderi. In median section from hinder edge to front the head of P. 533 is almost a quadrant of a circle; the lateral border stands vertically, the opercular (extra lateral of Traquair, 1904, fig. 34) being attached to its lower edge. The opercular of the left side is displaced outwards and backwards by being squeezed down on to the forward part of the anterior ventro-lateral and the arm plate; it is evidently complete, except for a fragment some 3 mm. in length which is stripped off the posterior end, leaving behind it an impression in the matrix. The outer surface of the anterior end of the opercular turns inwards almost through a quadrant of a circle, forming a nearly straight border. From this anterior region a very definite process passes upwards and inwards, and there is a matching facet on the lower border of the lateral plate of the head to accommodate it (text-fig. 1, *C*, *Fac. Art. Proc.*). The process is marked off from the rest of the plate by a distinct unornamented groove, clearly recessed below the outer surface of the bone by at least half a millimetre, and passes into the body of the bone without any change in the character of its ornamented surface. Behind this is the rounded notch shown in text-fig. 1, *C*, which has a cylindrical surface more than 2 mm. in width. It does not look like an articular surface, and seems in every way fitted to be filled with the projection *Proc.* (best seen on the right side) which lies quite laterally on the lateral plate; the rest of the dorsal border of the opercular fits exactly under the remaining ventral margin of the lateral plate. The implication is, therefore, that this plate was indeed a genuine opercular, hinged anteriorly but merely fitting against the hinder part of the lateral margin of the head shield. The upper border of the bone is comparatively thick, its lower border, very thin; it is clearly adapted to fit snugly down against the anterior ventro-lateral, thus making a watertight gill chamber.

Stensiö (1947, fig. 13) shows this opercular plate with an opening called 'spiracle', which is presumably the notch into which the lower projection of the lateral plate fits. It does not seem to me in the least likely that it is actually a spiracle: indeed to anyone handling my material such an idea would not occur at all. The spiracle in those fish in which it does occur lies anteriorly and dorsally, and does not form part of the border with which the opercular articulates. Stensiö's 'prelateral plate' (fig. 14) I have never seen: I strongly suspect it is, in fact, merely that part of the opercular which lies below the inwardly directed process by which the bone articulates with the head shield.

The opercular is absent on the right side, thus exposing some part of the almost flat floor, and the incomplete hinder surface of the gill chamber, which is carried entirely on the anterior ventro-lateral plate, and lies immediately in front of the helmet process. P. 625 shows very well the lower surface of part of the gill chamber, and the boss of bone containing the helmet process which is its vertical hinder wall (text-fig. 2, *E*). A pronounced ridge runs forwards and inwards from the boss, and represents the base of the median part of the hinder wall of the gill chamber on to whose posterior surface the trunk musculature was inserted.

Bothriolepis canadensis. The opercular of *B. canadensis*, shown in P. 101, agrees entirely in nature and relative size with that just described in the small Russian form. It shows the internal process, broken and incompletely exposed, behind which is an almost hemispherical notch of small size. The anterior part of its lower border is incomplete, but half-way along it is seen to be thin and very slightly rounded, tapering off until at the hinder end it is a feather edge.

Pterichthyodes. It is interesting to compare the character of the opercular of *Bothriolepis* with that of *Pterichthyodes*, which is represented in my collection by P. 339, a nodule from Tynet Burn, Nairn, showing a perfect mould of the visceral surface of the head, and the visceral surface and dorsal margin of the opercular, casts from which show all the details of its structure. The opercular differs noticeably from that of *Bothriolepis* because it has a long, straight dorsal border which was attached to the lateral border of the head shield, and is relatively longer and wider. Towards its hinder end, the thickened dorsal edge of the opercular bears a conical pit extending into its substance, which ends blindly, and is evidently related to some attachment to the head shield. C. 85 (U.C.L. collection), a similar specimen from Lethen Bar, Nairn, which has also been converted into a mould, is less well preserved but confirms the structure described above, though it adds nothing to it.

Asterolepis. In *Asterolepis* (P. 187) the head shield is narrow, and the eyes large and far forward. According to Gross (1931, pl. 12, fig. 7) the opercular is relatively even longer than in *Pterichthyodes* and is attached to the whole lateral border of the head shield; this conception is supported by the appearance of a rather badly preserved, very small specimen from Nairn (P. 67), probably the most complete *Asterolepis* known. It may be noted that Gross's figure shows a notch in the middle of the long upper border of the opercular which corresponds with the similar notch (the conical pit) in the upper border of the opercular of *Pterichthyodes*.

As I have shown above, it seems evident that the opercular bone of *Bothriolepis* was movable; indeed it may well have had considerable freedom, pivoting round the process from its anterior end which fits into the corresponding pit on the head shield. Its existence and character imply a fish-like set of respiratory movements. In other words the branchial arches must have been provided with a musculature capable of bringing about such rhythmical movements, alternately taking in and discharging water from the branchial region. This branchial region, evidently very short, is wide from side to side, and may well have been quite capacious because the whole head is broad.

The brain case of the antiarchs is practically unknown: Gross's figure of the dermal part of the head of *Asterolepis* (1931, pl. 12, fig. 7) shows in effect all that is known of it. The median nuchal plates of *Asterolepis* and *Bothriolepis* (Stensiö 1931, figs. 14–18), showing what appears to be the summit of a foramen magnum, suggests that it may have been comparatively large, and the visceral surface of the *Pterichthyodes* head shield represented by P. 339 bears this out. The brain must, however, have been a remarkable shape, for the confluence of the orbits above it suggests that it lay well down towards the roof of the mouth, of whose character we know nothing. In *Pterichthyodes*, at any rate, the bone forming the roof of the head is shown by the mould in P. 339 to have been extremely thick, a maximum in front of the orbits of 4 mm., in a head 30 mm. long.

The head of the antiarchs is thus known to some extent in a variety of forms of preservation. The position of the branchial arches in *Bothriolepis* is evident and any spiracular opening which existed could be expected to come out, either through a special opening in the head shield, or a notch in its border, which should, in the perfectly preserved material available, make some definite showing. In fact, in no such material is anything of the kind visible, and the obvious reading is that the first gill slit was of full size, and not reduced to its dorsal end alone. It would agree with the conditions which I believe exist in the Acanthodians, an association which is perfectly reasonable, for although there is little reflection of acanthodian structure elsewhere, there is evidently no countervailing resemblance to fish.

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